

THE ORIGIN OF AFRICAN PROTEACEAE

By J. S. BEARD

A recent paper by Levyns (4) in this Journal put forward evidence for a northern origin of the African Proteaceae. While unfortunately some of this evidence was based upon inaccurate data, it is possible at least partly to support the author upon other grounds.

A point is made that many of the tropical species of *Protea* show a very wide type of distribution and marked discontinuities within their range, whereas Cape species show a continuous type of distribution over a limited area. In fact, the discontinuities in the tropical species are more apparent than real. A false impression has arisen due partly to inadequate collecting in tropical Africa and partly to taxonomic confusion.

The three species cited by Levyns, *P. gagedi*, *P. madiensis* and *P. angolensis* together with *P. hirta* are the "big four" among tropical *Proteas* and are in fact to be found practically everywhere that there are *Brachystegia* woodlands. They are in fact "liable to be found throughout their range wherever a suitable habitat occurs" as in the case of Levyns' Cape species. There are no marked discontinuities except in the one case, the occurrence of *P. angolensis* in western West Africa without (and this is apparently reliable) anything else nearer than Angola.

The synonymy and distribution of these species are as follows:—

P. gagedi Gmel. = *P. abyssinica* Willd., *P. busseana* Engl., *P. chrysolepis* Engl. & Gilg, *P. leucoblepharis* (Welw. ex Hiern) Baker, *P. manikensis* de Wild, *P. ramosa* Hauman, *P. trigona* Phillips. Throughout *Brachystegia* belt at lower altitudes, on the east extending north to Eritrea and south to Zululand.

P. madiensis Oliv. = *P. bequaertii* de Wild. Central *Brachystegia* belt at higher altitudes, absent from S. Rhodesia, rare in Angola. Extending north into S. Sudan and across the Sudan region west to Nigeria.

P. angolensis Welw. is polymorphic: the aggregate species embraces *P. chionantha* Engl. & Gilg with vars., *P. bianoensis* de Wild., *P. homblei* de Wild., *P. trichanthera* Baker, *P. wangenheimii* Engl. Throughout the *Brachystegia* belt at middle elevations and in western West Africa.

P. hirta Klotzsch = *P. congensis* Engl., *P. eickii* Engl., *P. goetzeana* Engl., *P. kirkii* C. H. Wright, *P. melliodora* Engl. &

Gilg, *P. myrsinifolia* Engl., *P. swynnertonii* C. H. Wright, *P. uhehensis* Engl., *P. welwitschii* Engl.

Throughout the *Brachystegia* belt at middle to high elevations, extending north to Uganda and south to Transvaal and Natal.

The number of tropical species of *Protea* is thus much less than the 54 in the literature; there is also much reduction to synonymy among species other than those above. Confusion has been due to the high variability of the material. It is the writer's opinion that it is not possible to understand these plants adequately unless they are studied in the field.

Although Levyns' evidence for considering the tropical species of *Protea* as the older must be discounted, there is other evidence pointing to her conclusion. In general, there are two types of habitat characteristic of the tropical *Proteas*. One set of species occurs as undershrubs in *Brachystegia* woodland and they tend to be of wide range because the habitat is very extensive. A second group consists of components of an ericaceous mountain woodland or scrub, at higher elevations than the former group. As is usual in mountain floras the species tend to be localized rather than of wide distribution. Sometimes the ericaceous zone is intact, sometimes it has been destroyed or damaged by fire, in which case the *Proteas*, being fire resistant, may be left as survivors in mountain grassland. They may even be led to become more abundant and to form parklands by themselves, like *P. madiensis* on the Vipya highland in Nyasaland. There is no particular morphological distinction between the species of the two habitats. Tropical *Proteas* belong either to Phillips' sections *Lasiocephalae* and *Leiocephalae* or to the new section *Patentiflorae* Beard (1), which are poorly represented in the Cape flora, while none of the other sections of the genus occur outside the Cape fynbos except for one species of *Ligulatae* and two of *Exsertae*, which are found in the summer rainfall area of the Union. There is thus quite a strong morphological distinction between tropical and Cape *Proteas*.

It is considered that there are good grounds for the view that many of the tropical species, in particular those of the *Patentiflorae*, are less highly evolved than those of typical Cape sections of the genus and are thus more primitive. Before going into detail, some reference is necessary to other *Proteaceous* genera. Levyns shows that there are fourteen genera of the family in Africa, of which eleven are confined to the western Cape, one (*Protea*) occurs about as abundantly outside the Cape flora as in it, one (*Leucospermum*) has a single extra-Cape species reaching Rhodesia, and one (*Faurea*) is confined to tropical and sub-tropical Africa and

Madagascar. If we examine the inflorescences of these genera it must be concluded that that of *Faurea* is apparently the most primitive, consisting of a long spike along which the flowers are laxly arranged. Evolution in the family appears to have led to progressive compression of the spike with the flowers increasingly crowded, first into a short spike as in some species of *Leucospermum*, *Paranomus*, *Mimetes*, etc., then into dense heads with the receptacle at first elongated or conical, later flattened, later still (or as a separate evolutionary line) with bracts to enclose the flowers. Other evolutionary trends that we may distinguish are the introduction of dioecism as in *Leucadendron* and the transition from trees, as in *Faurea*, to shrubs of smaller and smaller stature ending as low woody plants with ephemeral shoots emitted from an underground rootstock.

Within the genus *Protea* itself we may distinguish many of these evolutionary trends. It is considered that the section *Patentiflorae* contains the most primitive species. Certain of them (*P. rubropilosa*, *P. comptonii*, *P. curvata*, *P. rupestris*) have a markedly conical receptacle in the flower head, they are small erect trees whose habit suggests *Faurea* rather than *Protea*, and their distribution suggests that they are ancient, relict species. Other *Patentiflorae* have only a convex receptacle, are small spreading trees and shrubs and have a wide distribution. All of them share the character which gives the name to the section and is itself considered primitive, namely *eversion* of the flower head. The bracts function only as bud scales and once the head has opened at anthesis it remains wide open until the seed is shed. The heads are large and showy and they open widely, at least to 180°, sometimes more. In *P. rupestris* (syn. *P. bella*) the bracts reflex completely and recall the behaviour of *Leucospermum reflexum*. Typical members of this group of *Patentiflorae* are *P. angolensis*, *P. madiensis* and *P. elliottii*.

The sections *Lasiocephalae* and *Leiocephalae* suggest some evolutionary advance, as the bracts have an additional protective function. After anthesis the heads close once more, the bracts coming together as in bud, and remain closed while the seeds are ripening. Eventually they open again and the seeds are blown away. There is also some reduction of head size and showiness. Many of them are shrubs or sub-shrubs. The *Lasiocephalae* have retained the primitive character of hairy flowers while the *Leiocephalae* largely discard it.

The tropical *Proteas* appear to show evidence of a slow, steady evolution extending over a very long period and together with the occurrence of primitive *Faurea* suggest that the *Proteaceae* have an ancient history in Central Africa. The Cape members of the family on the other hand seem to suggest rather a relatively recent exuberant out-

burst of speciation. Considering again the case of *Protea*, many of the Cape species are specialized mountain plants which must have developed close adaptations to harsh local environments, probably over quite a long period. The species of lower elevations, however, by their multiplicity, their exuberance, and the extraordinary developments of their floral parts which sometimes border on the fantastic and seem to be purely non-adaptive, suggest the filling of some floristic vacuum.

How could this have occurred? Good (3), in a recent paper in *Nature*, has outlined a probable course of floristic development in Australia associated with the likely movements of that continent since the disruption of Gondwanaland. A similar construction for the African continent may be informative.

It is pointed out by Good that the Australian flora contains three main elements: an "Afro-Australian" element, in which the Proteaceae are prominent, a "south circumpolar" rain-forest element and a "Melanesian" rain-forest element. Southern Africa contains an Afro-Australian element, lacks the south circumpolar rain-forest element, and has a tropical African rain-forest element which behaves in a similar manner to the Melanesian in Australia, extending south and westwards along the east coast and becoming progressively impoverished in species as it does so. Southern Africa also has an endemic desert flora which has no real counterpart in Australia.

Evidence from the movements of the ice sheets which deposited the Dwyka tillite (? U. carboniferous) indicate that Southern Africa then lay over the South Pole (or that the Pole then lay in S. Africa). During subsequent Permian and Triassic times progressively warmer conditions seem to have prevailed. According to Du Toit's (2) reconstruction of the movements of Africa since the disruption of Gondwanaland, the continent moved to the north until it came into contact with the land-mass of Europe, after which there was a retreat to the southward. The southern parts of Africa therefore first became progressively warmer and less under the influence of the belt of westerly winds, and the weather regime changed probably entirely to one of summer rain. Later, with the southerly movement of the continent, the southern coast became once more subject to the westerlies.

The flora of Southern Africa, if basically Afro-Australian at the close of the Mesozoic period and characteristic of a moist, warm-temperate climate such as is found to-day in latitudes 30°—40° S., would have had either to adapt itself to tropical and sub-tropical conditions or take refuge in the mountains. The original warm-temperate lowland flora (including the south circumpolar rain forest flora) would have been exterminated. Later as conditions grew again more temperate there was no

land to the southwards from which plants suited to the new conditions could immigrate, leading to a floristic vacuum, a condition, we may suppose, encouraging to the formation of new species.

It is apparent that the ancestors of the present Afro-Australian flora must have been established in the southern hemisphere while Africa and Australia were still in contact since although Africa could very well have received this flora from the north at a later date it is impossible to see how Australia could have done so. It is also a reasonable assumption that it was a warm-temperate flora. Among the Proteaceae, *Faurea*, the most primitive genus, inhabits tropical bush towards its upper altitudinal limits and its ancestors must have originated or adapted themselves there. The most primitive *Proteas* that we can trace occur along the ecotone between tropical bushveld and montane ericaceous bush or grassland. This zone lies closest to the environment of a more southerly warm-temperate flora. The adaptations of newer species may be supposed to have led them into the higher levels of tropical bush on the one hand and into the montane zone on the other.

When the southward movement of Africa provided a cool, moist lowland habitat along the southern and south-western coast the obvious source of plants to colonize it would be the upper mountain areas, already plentifully endowed with Proteaceae, Ericaceae and so on. In descending to lower altitudes to fill the vacuum it is logical that an exuberant outburst of speciation may have occurred. While the flora of the south-western Cape seems therefore to be basically of southern origin, it would be so at second hand, so to speak, being derived directly from a tropical montane flora that may have had its origin in Gondwanaland.

REFERENCES.

1. BEARD, J. S. The Genus *Protea* in the Summer-Rainfall Area of the Union. *Bothalia* 7: 41-63. 1958.
2. DU TOIT, A. L. Our Wandering Continents. 1937.
3. GOOD, R. The Biogeography of Australia. *Nature* 4626, pp. 1763-5. 1958.
4. LEVYNS, M. R. The Phytogeography of Members of Proteaceae in Africa. *Jour. S. Af. Bot.* 24, pp. 1-9. 1958.